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THE MIOCENE LEMUROIDS OF EAST AFRICA

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INTRODUCTION

The fossil lemuroid material to be described was discovered in Kenya Colony, on Rusinga Island in the Kavirondo Gulf of Lake Victoria and at Songhor. With the exception of the holotype of *Progalago dorae,* the material was collected by Dr. L. S. B. Leakey and members of the British-Kenya Miocene Expedition during the period 1947 to 1950. All the fossil specimens were obtained from sites believed on the faunal evidence to be of early Miocene age (see Le Gros Clark & Leakey, 1951). The collection consists of mandibular and maxillary fragments and a brain case with a natural endocranial cast. The material is all referable to the infra-order Lorisiformes, sub-family Galaginae. Previously, our knowledge of the early Galaginae was limited to a single specimen, an isolated jaw fragment from Songhor, containing P$\overline{4}$ and M$\overline{2}$. MacInnes (1943) showed that in the morphological details of the dentition this specimen conforms with the Galaginae rather than the Lorisinae. He assigned it to a new genus *Progalago* which he suggested might be directly ancestral to the modern galagos. Lewis (1933) founded the genus *Indraloris* on an isolated second lower molar from the Lower Middle Siwalik horizon of North India. This specimen is the sole fossil representative of the Lorisinae, and Lewis considered *Indraloris* to be the probable precursor of the Recent lorises. Until the recent discoveries in Kenya, only these two fossil representatives of the Lorisiformes, both based on isolated specimens, had been described.

The present collection contains specimens closely resembling the holotype of *P. dorae* in their dentition. Several of them are considered to belong to that species, whereas others are regarded as specifically distinct.

Holotypes of new species are in the Geological Department of the British Museum (Natural History). Other individual specimens are referred to by the provisional numbers given to them in the field during each season's work of the British-Kenya Miocene Expedition. In the case of the material found on Rusinga Island, the field number of each specimen is followed by the site (in brackets). The site numbers R1 to R113 refer to sites whose position is shown on the map in Le Gros Clark & Leakey (1951, p. 9).

The following prosimian material has been used for comparative studies of the skull and dentition: *Galago crassicaudatus*: *G. c. garnetti*, *G. c. panganiensis*, *G. c. crassicaudatus*, *G. c. monteiri*, *G. c. hindei* (*lasiotis*); *Galago senegalensis*: *G. s. braccatus*, *G. s. albipes*; *Galago demidovii*: *G. d. thomasi*, *G. d. demidovii*; *Nycticebus coucang borneanus*: *N.* sp.; *Arctocebus calabarensis*; *Perodicticus ibeanus*; *Loris gracilis*; *Microcebus coquereli*; *Cheirogaleus major*; *Lemur coronata*; *Tarsius spectrum*.

Genus *PROGALAGO* MacInnes

The original diagnosis of this genus (MacInnes, 1943: 145) is: "A lemuroid in which the lower $Pm\overline{4}$ is monocuspid, the hypoconid being practically undeveloped. Greatest depth of horizontal ramus of mandible below $M\overline{3}$. Lower dental formula probably 2:1:3:3."

The additional material enables MacInnes' diagnosis to be extended and modified. Thus his estimate of the dental formula is substantiated, but the fact that the greatest depth of the horizontal ramus is at the level of $M\overline{3}$ is considered here to be of specific rather than of generic value.

The incisors and canine of this genus show some degree of procumbency. The lower margin of the symphysis extends downwards in the mid-line to form a tubercle which projects well below the level of the inferior border of the ramus. $P\overline{4}$ is predominantly monocuspid with slight indications of the hypoconid and metaconid; there is a large posterior talonid. The long axis of $P\overline{4}$ is set more obliquely to the line of the other teeth than in the modern galagos. $M\overline{2}$ is quadricuspid with the protoconid and hypoconid slightly anterior to the metaconid and entoconid respectively. The distance between the hypoconid and the entoconid exceeds that between the protoconid and metaconid. From the apex of the hypoconid a sharp crest extends downwards, inwards and forwards to the base of the protoconid; there is a well-marked trigonid with an interior cingulum, but no paraconid is present. Other features of this genus are a prominent hypoconulid on $M\overline{3}$ and a well-developed entoconid on the lower molars.

Progalago dorae MacInnes

(1943: 145)

(Pl. **2**, figs. 4, 5; Pl. **3**, figs. 6–11; Text-fig. 1)

Amended Diagnosis.—The mandibular depth increases from front to back, and is greatest at the level of $M\overline{3}$. Length of lower molar series approximately 11 mm. Weakly developed external cingulum on the anterior part of the lower molars. Upper molars show a simple trigon with cusps of approximately equal size. There is a small hypocone on $M\underline{2}$.

Holotype.—Part of a left horizontal mandibular ramus, containing $P\overline{4}$ and $M\overline{2}$. Brit. Mus. (Nat. Hist.), M.16907. (Field No. *S*.9, 1938.)

Horizon.—Lower Miocene.

Locality.—Songhor, Kenya Colony.

Description and Remarks.—*P. dorae* is now represented by 10 specimens, including the holotype. The only two maxillary fragments of *Progalago* so far found have been assigned to this species.

MANDIBLES AND LOWER TEETH

S.310, 1949 (Pl. 3, fig. 6).—A small mandibular fragment of the right side containing three quite unworn and undamaged premolars. Anteriorly the lower part of the canine socket is present and, immediately in front of and below this, there is a small impression of the lowest part of the lateral incisor socket. The inferior border of the ramus begins to show an inward curve just behind the anterior fracture line, and at the extreme antero-inferior point of the fragment there is a slight but distinct downward projection of the bone. In the holotype (Pl. 2, figs. 4, 5) this projection develops more anteriorly into a definite tubercle at the lower border of the symphysis. The mental foramen is situated below the middle of the ramus, slightly behind the level of the anterior border of $P\overline{4}$.

Sufficient of the canine socket is present to determine that it inclines forwards, indicating that the canine was at least partially procumbent. The inclination of the very incomplete socket of the lateral incisor suggests that this tooth also had developed some degree of procumbency. In the modern Lorisiformes the shelf of bone in the symphysial region, behind the procumbent incisors and canines, slopes gently backwards and downwards; in the fossil specimen, the slope of the corresponding region is considerably steeper. This is probably correlated with the relative degree of procumbency of the incisors and canines, and may indicate that in *Progalago* these teeth had not developed the extreme procumbency seen in the modern Lorisiformes.

The most anterior tooth is an intact $P\overline{2}$, the crown of which projects above the level of the other two premolars; this projection, however, tends to be more marked in the modern galagos, and the tooth does not possess the sharp dagger-like crown of the latter. The anterior border has a forward angulation which gives the crown a quadrate form from its lateral aspect, and a very well-defined internal cingulum passes downwards and medially from it. The protoconid is set on the lateral side of the crown, and the posterior border slopes backwards from it. A slight swelling at the base of the posterior border represents an incipient talonid. The tooth as a whole is set in the mandible laterally to the line of the other two premolars. This lateral displacement of $P\overline{2}$, which does not appear to be due to post-mortem distortion, has not been observed to a comparable extent in the Recent galagos examined.

Except that it is smaller, $P\overline{3}$ resembles $P\overline{2}$, and the anterior border exhibits the same marked forward angulation. The crown is flattened in a lateral direction, and is somewhat spatulate in form. The internal cingulum is not so pronounced, but is well developed posteriorly. The crowns of both $P\overline{2}$ and $P\overline{3}$ are inclined somewhat forwards, resembling in this respect the procumbency seen in the corresponding teeth of *Necrolemur*. The crown of $P\overline{3}$ projects to a higher level than $P\overline{4}$.

$P\overline{4}$ is predominantly monocuspid, but it possesses a large talonid. The obliquity of its long axis to the line of the alveolar margin, which MacInnes noted in the holotype, is not so conspicuous a feature in this specimen. From the apex of the protoconid a well-defined crest passes to the antero-external angle, and the anterior border of the tooth shows the same pronounced forward convexity seen in the other two premolars. A very small hypoconid surmounts the hollowed-out talonid basin postero-laterally, at the base of the protoconid. It is not developed to the extent seen in the modern galagos, but it is more pronounced than the incipient hypoconid in the $P\overline{4}$ of the holotype. There is also a slight swelling of the cingulum at the postero-internal angle of the tooth, which possibly represents an entoconid. A crest extends downwards from the apex of the protoconid to the middle of the inner margin of the tooth, and on it there is a small elevation near the protoconid. The tooth as a whole shows a definite tendency towards molarization, a condition which is found to a much greater degree in the galagos of today.

S.104, 1948.—A right mandibular fragment containing two worn premolars, $P\overline{2}$ and $P\overline{3}$. Immediately anterior to $P\overline{2}$ the ramus is fractured, partially exposing the single, well-developed root of the tooth. This specimen also shows a small downwardly projecting tubercle situated at the lower border of the symphysis.

The apices of the crowns of $P\overline{2}$ and $P\overline{3}$ are worn away. The teeth present the same general features noted in specimen *S*.310 but they are slightly larger, and $P\overline{3}$ has a rather more pronounced talonid. The internal cingulum is well developed on both premolars. The posterior part of the fragment contains the root sockets of $P\overline{4}$, $M\overline{1}$ and $M\overline{2}$, and a socket for one of the roots of $M\overline{3}$. The mental foramen is situated below the middle of the ramus at the level of the posterior part of $P\overline{3}$. Immediately above and behind it there is a much smaller accessory foramen.

R.516, 1949 (Site R3a).—An isolated intact lower left $P\overline{2}$. It shows particularly well the marked convexity of the anterior border, the pronounced internal cingulum and the incipient talonid. The root is relatively long and somewhat flattened in a lateral direction.

R.649, 1949 (Site R3a).—An isolated lower left $P\overline{2}$ similar to but larger than the other specimens.

S.10, 1949 (Pl. 3, figs. 7, 8).—A fragment of a mandible containing the two posterior lower left molars ($M\overline{2}$ and $M\overline{3}$). The ramus shows clearly the progressive increase in depth of the mandible from front to back. The condition in the modern galagos, where there is commonly a slight decrease in the depth of the mandible posteriorly, is in marked contrast to this. Anteriorly, the ramus of the mandible is broken off, exposing the anterior root of $M\overline{2}$. The fragment includes a small portion of the ascending ramus posteriorly, and part of the inferior border of the horizontal ramus is also intact.

$M\overline{2}$ is somewhat smaller than the corresponding tooth in the holotype, but is otherwise similar. Thus it is quadricuspid, with the hypoconid and entoconid set slightly wider apart than the protoconid and metaconid. The two inner cusps are situated just behind the levels of the corresponding outer cusps. A well-defined crest runs from the apex of the hypoconid inwards and forwards to the medial side of the base of the protoconid. Crests also connect the metaconid and entoconid, the hypoconid and entoconid, and the protoconid and metaconid. Lastly, two small crests pass forward from the metaconid and protoconid to join the prominent anterior cingulum. The external cingulum is moderately developed, being rather more conspicuous anteriorly.

$M\overline{3}$ possesses a large and prominent hypoconulid, situated slightly to the inner side of the median axis of the tooth. The hypoconulid projects a little above the level of the other cusps, and is relatively more pronounced than it usually is in the modern galagos. A further point of interest is that the entoconid is equal in size to the other cusps. In the modern galagos the entoconid of M$\overline{3}$ tends to be reduced; indeed, in none of the present-day galagos examined has it been found to be so well developed as it is in *Progalago* (Pl. 3, fig. 11), whereas the third lower molars of *Loris*, *Nycticebus* and *Arctocebus* possess a well-developed hypoconulid and entoconid.

In the modern galagos M$\overline{3}$ tends to be reduced in size in comparison with M$\overline{2}$, whereas in this fossil specimen M$\overline{3}$ is greater in length than M$\overline{2}$ and is only very slightly less in width. In all other features, M$\overline{3}$ closely resembles M$\overline{2}$.

S.81, 1947.—The upper part of a mandibular ramus, containing the two posterior lower left molars. The teeth are worn, and part of the lingual surface of M$\overline{2}$ has been eroded away.

R.608, 1949 (Site R1a).—Part of the horizontal ramus of a lower jaw, distorted by a vertical fracture about half-way along its length. The three molars have been severely eroded, and, more anteriorly, the lower parts of the sockets of P$\overline{2}$ and P$\overline{3}$ have been exposed. Unfortunately at the base of the symphysial region the whole of the alveolar margin and the upper part of the body are missing. As in other specimens, there is a small downwardly projecting tubercle at the lower margin of the symphysis. Except for M$\overline{2}$, the teeth are too incomplete either for measurement or for description. This latter tooth, although somewhat larger in size, presents essentially the same features noted in the other specimens of *P. dorae*.

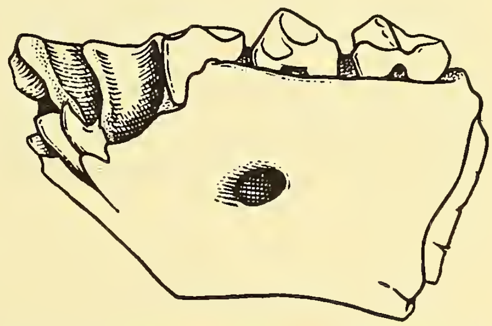

Fig. 1. Fragment of the left side of a mandible of *P. dorae* (*R*.167, 1951). ×5. The crowns of P$\overline{3}$, P$\overline{4}$ and M$\overline{1}$ are badly damaged. The sockets for the canine and P$\overline{2}$ are seen, as well as the lower ends of the roots of the canine and the two incisors. The canine and incisors were evidently procumbent, but not to the degree found in modern Lorisiformes.

R.167, 1951 (Kathwanga) (Text-fig. 1).—The anterior portion of a left mandibular ramus. P$\overline{3}$, P$\overline{4}$ and M$\overline{1}$ are preserved, but their crowns have been badly eroded, obscuring the details of the cusp pattern. The bony sockets for the roots of P$\overline{2}$ and the canine are exposed, although the outer walls of the sockets are missing. The socket for P$\overline{2}$ is relatively large, indicating a strong and somewhat caniniform tooth. This agrees with the other specimens of *Progalago* in which P$\overline{2}$ is preserved. The socket also shows that the tooth had only one root. In modern galagos, the root of P$\overline{2}$ overlaps the root of the canine laterally, so that the latter is antero-medial rather than directly anterior to the premolar. As far as can be judged from the incomplete sockets of the fossil specimen, the canine was more directly anterior. It is probable, therefore, that the canine was not completely taken over into the incisor series as it has been in the modern galagos, but, until more complete specimens of the symphysial region of the mandible of *Progalago* are available, the precise relationship of the canine to the incisor teeth remains in some doubt.

The canine socket is much smaller than the P$\overline{2}$ socket; at its lowest part a fragment of the tooth remains in position. Immediately in front of the canine socket the lower part of the lateral incisor is exposed. Medial to and in front of the lateral incisor root, a small portion of the medial incisor root is also exposed. By their forward inclination, these root fragments clearly show that the incisors and canine were procumbent. It is equally clear, however, that the procumbency of the front teeth was not as marked as in the modern galagos. This corroborates very well the more indirect evidence regarding the inclination of the front teeth obtained from other specimens of *Progalago*. An examination of the roots of the lateral and medial incisors also shows that the lateral incisor root was the larger of the two. In the modern galagos examined, the lateral and medial incisor teeth are of approximately the same size.

The large mental foramen in specimen *R*.167, 1951, at the level of the anterior border of P$\overline{4}$, is commonly found in this situation in the other specimens of *Progalago* and also in the modern galagos. Posteriorly, the lower border of the mandible begins to curve downwards; this strongly suggests that when intact the mandible must have increased in depth posteriorly. The fossil specimen would thus appear to belong to *P. dorae*, and this reference is confirmed by certain other features. Thus the teeth, in spite of their poor preservation, show a fairly close general resemblance to *P. dorae*, cf. specimen *S*.310, 1949, in which the three premolars are present. The depth of the mandible at the level of P$\overline{4}$ is approximately the same in both specimens. Unfortunately, the teeth are too badly eroded for accurate measurement. However, the estimated measurements conform well with those of the corresponding teeth of *P. dorae*.

MAXILLAE

R.106, 1948 (*Surface find*) (Pl. 3, fig. 10).—One of the only two maxillary fragments of *Progalago* so far discovered; it contains the two posterior left molars. M$\underline{2}$ is slightly damaged, but the disposition of the cusps can be seen. The trigon is well defined, and the three cusps are of approximately equal size. Low crests join the protocone to the paracone and to the metacone. Postero-medially to the protocone there is an internal cingulum, with a small cingulum-hypocone. The apex of the hypocone is missing, however, and the full extent of its development cannot be judged.

In the modern galagos, the two anterior upper molars possess a conspicuous notch in their posterior margin. Particularly noticeable in M$\underline{1}$ and M$\underline{2}$, it can also be seen to a lesser extent in P$\underline{4}$. This notch is a V-shaped indentation between the metacone and hypocone caused in large part by the development of a prominent cingulum-hypocone, postero-medial to the protocone. In the fossil specimen, M$\underline{2}$ possesses a slight notch in its posterior border, but this is an artefact caused by post-mortem damage to the tooth. Indeed, careful study makes it clear that the fossil differs from the modern galagos in the absence of the notch, and resembles the modern Lorisinae much more closely. In the latter, also, there is a relatively less well-developed cingulum-hypocone.

M$\underline{3}$ consists solely of the primitive trigon; it possesses neither an internal cingulum nor a hypocone. The metacone is somewhat smaller than the corresponding cusp on M$\underline{2}$. M$\underline{3}$ is but little smaller than M$\underline{2}$ and, apart from the points just mentioned, there are no significant differences between the two teeth. M$\underline{3}$ does not exhibit the degree of reduction in size compared with M$\underline{2}$ commonly seen in the galagos of today.

In addition to the teeth, this fragment retains the base of the zygomatic process of the maxilla, which is situated immediately lateral to and above the two molars. The process itself is largely intact, and its form and position present some interesting features. The specimen has been broken immediately behind the zygomatico-maxillary articulation, but the suture can only be perceived with difficulty. It is quite apparent, even from so small a fragment, that the zygomatic process did not project laterally to the extent seen in some of the modern Lorisiformes; possibly the eyes were relatively smaller in size, or were somewhat more laterally directed. Another feature in which the fossil differs from the modern forms is that the zygomatic process projects from the body of the maxilla rather more posteriorly in relation to the position of the teeth. Consequently, it is joined directly to the alveolar margin as far back as the level of the posterior border of $M\underline{3}$. This condition has not been observed in any of the modern Lorisiformes examined: in them the zygomatic process is connected directly to the alveolar margin as far back as the anterior border or, occasionally, at most the middle of $M\underline{3}$.

Finally, although only the commencement of the zygomatic arch is present, there is sufficient to show that it was very slender, especially in relation to the size of the teeth. The maximum vertical width of the arch in the fossil is only 3·3 mm. In those specimens of galagos that have molars of comparable size, the minimum vertical width of the zygomatic arch at its maxillary commencement has not been observed to be less than 4 mm. As a corollary, in the fossil the lower margin of the bony orbit is relatively nearer to the cheek-teeth than it is in the modern galagos.

It may be inferred from the maxillary region of the zygomatic arch that the facial part of the skull was more lightly constructed than in the modern Galaginae. The two molars are of a relatively primitive type, and in certain structural details, such as the relative development of the hypocone on $M\underline{2}$ and the degree of reduction of $M\underline{3}$ relative to $M\underline{2}$, they show greater resemblances to *Nycticebus* than to the modern galagos.

S.93, 1948 (Pl. 3, fig. 9).—Approximately the anterior half of the lateral surface of a right maxilla, together with the anterior two premolars, the canine, and the remains of the lateral incisor. At the anterior extremity of the fragment is a small portion of the premaxilla, but the premaxillo-maxillary suture is indistinct. The specimen ends immediately behind $P\underline{3}$; on its medial aspect a small lateral portion of the palate is present.

The lateral incisor and canine have both been damaged, and little more than the stumps of the teeth remain. $P\underline{2}$ and $P\underline{3}$ also show very distinct signs of wear. The lateral incisor was evidently a small styliform tooth similar to that of most of the modern Lorisiformes, but it did not show the extreme reduction seen in *Nycticebus*. Although a large part of the canine is missing, sufficient remains to indicate that the tooth was not very large. Indeed, by comparison with the canines of modern galagos possessing premolars of approximately the same size as those of specimen *S*.93, it appears to have been somewhat reduced.

Between the canine and $P\underline{2}$ there is a conspicuous diastema, 1·4 mm. wide. None of the modern galagos examined has so large a diastema, though in *Nycticebus* the distance between the two teeth has been observed to reach 1·6 mm.

TABLE 1

MANDIBLE AND LOWER DENTITION OF *PROGALAGO*

(Measurements in mm.)

		Body of Mandible		Length of Molar Series	P2			P3			P4			M1			M2			M3		
		Ht. at level of P4	Max. thickness		a.p.	tr.	ind.	a.p.	tr.	ind.	a.p.	tr.	ind.	a.p.	tr.	ind.	a.p.	tr.	ind.	a.p.	tr.	ind.
P. dorae	*S*.310, '49	5·7	2·7		2·9	2·0	69·0	2·9	1·7	58·6	3·3	2·1	63·6									
	S.104, '48	7·5	3·5		3·0	2·1	70·0	3·0	1·7	56·7												
	S.516, '49				3·0	2·2	73·3															
	R.649, '49				3·7	2·7	73·0															
	S.10, '49		2·9														3·1	2·8	90·3	4·1	2·6	63·4
	S.81, '47																3·1	2·7	87·1	3·9	2·3	59·0
	R.608, '49		3·4														3·8	3·4	89·5			
	Holotype	7·0	3·5	11·5 (est.)							3·4	2·2	64·7	3·2 (est.)			3·6	3·3	91·7			
P. robustus	M.16876	4·3	2·4					2·2			2·5	1·6	64·0	2·4	2·0	83·3	2·6	2·2				
	S.8, '48		2·1																	3·4	2·0	58·8
	S.102, '48	4·7	2·6								2·4	1·6	66·7	2·6	2·2	84·6	2·7	2·3	85·2			
	R.618, '50		2·7	9·4										2·9	2·4	82·7	3·0	2·4	80·0	3·5	2·1	60·0
P. minor	M.16877		2·0	6·9										2·1	1·7	81·0	2·3	1·8	78·3	2·5	1·6	64·0
	R.611, '49		1·7												1·6		2·2	1·7	77·3	2·5	1·5	60·0

TABLE 2

UPPER DENTITION OF *PROGALAGO DORAE*

	P2			P3			M2			M3		
	a.p.	tr.	ind.	a.p.	tr.	ind.	a.p.	tr.	ind.	a.p.	tr.	ind.
R.106, '48 . .							2·9	4·1	141·4	2·5	3·8	152·0
S.93, '48 . .	3·2	1·5	46·9	2·9	1·8	62·1						

P2 exceeds P3 in length, resembling in this respect the modern Lorisiformes; it is a relatively narrow tooth, caniniform in type and possessing two roots. It has a single large cusp, the apex of which has been worn away. P3 is more triangular in plan and there is an additional postero-internal root. At the extremities of the anterior and posterior borders of the tooth small cuspules are developed. Similar cuspules, largely worn away, are present on P2.

Progalago robustus sp. nov.

(Pl. 3, figs. 12, 14–16)

Diagnosis.—The mandible does not increase in depth posteriorly. The size of the teeth falls below the range of variation in size of the corresponding teeth in the specimens of *P. dorae* so far discovered, but the indices of the teeth measurements are well within the *P. dorae* range. Length of lower molar series less than 10 mm. No external cingulum present. $P\overline{4}$ slightly more molariform than in *P. dorae*.

Holotype.—Part of a right horizontal ramus of a mandible, containing $P\overline{3}$, $P\overline{4}$, $M\overline{1}$ and $M\overline{2}$. Brit. Mus. (Nat. Hist.), M.16876. (Field No. *S*.390, 1949.)

Locality.—Songhor, Kenya Colony.

Horizon.—Lower Miocene.

Description and Remarks.—This species is represented by four specimens. The dimensions of the teeth and jaws are intermediate between those of the somewhat larger *P. dorae* and the much smaller *P. minor*.

M.16876 (Holotype: Pl. 3, figs. 14, 16).—The anterior portion of a right mandible. The lower part of the symphysial region is undamaged, and portions of the incisor, canine and anterior premolar sockets are present although the alveolar margin is missing. The crown of $P\overline{3}$ is missing, but $P\overline{4}$, $M\overline{1}$ and $M\overline{2}$ are intact and unworn.

Anteriorly, on the inner aspect of the ramus, the position of the symphysis is represented by a slightly elevated, oval area that slopes forwards and upwards, and has a small, downward-projecting tubercle at its postero-inferior extremity. Lateral to the symphysis are the lower parts of the sockets for the incisors, canine and $P\overline{2}$. The two incisor sockets are small, narrow and close together. The canine socket, situated more posteriorly, is approximately equal in size to both incisor sockets combined. Still more posteriorly, there is a comparatively large socket for $P\overline{2}$. From the shape and position of these sockets, it seems justifiable to infer that the incisors were narrow and close together, and that the canine had probably been taken over into the incisor series as in modern lemurs, at least to some extent. $P\overline{2}$ must have been a fairly large tooth and probably projected above the level of the other premolars.

The slope of the incisor and canine sockets indicates that these teeth must have been at least partially procumbent, but the downward slope of the symphysial region contrasts markedly with the much more nearly horizontal slope of the symphysial region in the modern galagos. This confirms the inference based on specimens *S*.301, 1949 and *R*.167, 1951 of *P. dorae* that, while the incisors and canines in *Progalago* were procumbent, they had not developed this condition to the extent seen in the galagos of today.

$P\overline{3}$ is incomplete: the crown has been broken off, but sufficient of the tooth is present to show that its long axis is placed obliquely in relation to the line of the tooth row, with its anterior extremity pointing somewhat laterally and the posterior extremity medially. $P\overline{4}$ exhibits some degree of molarization. The tooth as a whole is rather elongated, with the long axis disposed slightly obliquely to the line of the molars. The protoconid is situated towards the outer side of the crown, with a small cuspule on its medial aspect representing the metaconid. There is a well-defined, low talonid, with two small cusps surmounting it posteriorly. The outer cusp, or hypoconid, is better defined and projects to a higher level than the slightly more posterior inner cusp, or entoconid. The sharp, convex anterior border of the tooth passes from the apex of the protoconid to the antero-external angle of the tooth, where there is a slight projection. From the antero-external angle, a well-developed anterior cingulum passes medially and backwards, so defining the antero-medial border of the trigonid. Although this tooth is not molariform to the extent commonly found in $\mathrm{P}\overline{4}$ of the modern galagos, it nevertheless approaches the condition seen in the latter, and in this particular fossil specimen the only difference between the two appears to be one of relative development.

The first two molars are also present. They are perfectly preserved and show very well the details of the arrangement of the cusps and interconnecting crests (Pl. 3, fig. 16). In all essential features they resemble the molar cusp pattern of *P. dorae.*

R.618, 1950 (Gumba) (Pl. 3, fig. 15).—A fragment of the right mandibular ramus with the three molars. It is fractured immediately in front of $\mathrm{M}\overline{1}$; posteriorly the commencement of the ascending ramus is present. The inferior border of the horizontal ramus is undamaged along the entire length of the fragment, making it quite certain that the depth of the mandible between $\mathrm{M}\overline{1}$ and $\mathrm{M}\overline{3}$ is practically constant. Although the molars are somewhat weathered, it can be clearly seen that their general shape, and the arrangement of the cusps and interconnecting crests, are essentially similar to the molars of *P. dorae,* but they are smaller and there is no external cingulum.

The protoconid and metaconid in $\mathrm{M}\overline{1}$ are closer together than are the hypoconid and entoconid. This feature is not so distinct in $\mathrm{M}\overline{2}$, and even less so in $\mathrm{M}\overline{3}$. Each molar possesses a fairly well developed trigonid, especially $\mathrm{M}\overline{2}$ but, although the antero-external angle is prominent, there is no paraconid. The anterior cingulum is moderately developed. The outer cusps on all three molars are more sharply conical and less worn than the inner cusps. $\mathrm{M}\overline{3}$ possesses a large, well-developed hypoconulid situated slightly to the inner side of the median axis of the tooth. The somewhat worn entoconid on $\mathrm{M}\overline{3}$ is developed to the same degree as the other cusps. $\mathrm{M}\overline{3}$ is longer but rather narrower than the other molars and is not reduced in any way. The depth of the mandible at the level of the posterior border of $\mathrm{M}\overline{3}$ is 5·8 mm. The corresponding measurement in the smaller of the two comparable specimens of *P. dorae* (*S*.10, 1949) is 8·5 mm. As this is the largest of the specimens assigned to *P. robustus*, it is apparent that not only does that species differ from *P. dorae* in that the mandible does not increase in depth posteriorly, but there is also a significant difference in the depth of the ramus at the level of $\mathrm{M}\overline{3}$.

S.102, 1948.—Part of the left half of a mandible, containing $\mathrm{P}\overline{4}$ and the anterior two molars. The horizontal ramus has been broken off posterior to $\mathrm{M}\overline{2}$, and anteriorly a single $\mathrm{P}\overline{3}$ root-socket is present just behind the anterior fracture line. The crowns of the teeth in this specimen show evident signs of wear. However, they are similar in structure and possess measurements very close to the corresponding teeth in *S*.390, 1949. Neither in this specimen nor in *S*.390 is there any indication that the mandible increases in depth posteriorly. Immediately below the middle of the outer surface of the ramus, at the level of the anterior border of $P\overline{4}$, there is a distinct mental foramen.

S.8, 1947 (Pl. 3, fig. 12).—This is the posterior portion of the right side of a mandible in which the coronoid process is largely preserved, although the entire condyloid process is missing. The anterior fracture line is approximately 1 mm. in front of $M\overline{3}$ the only tooth present in the fragment. The posterior part of this tooth is damaged, and the entoconid is missing. It is thus difficult to compare it with the third lower molars of other specimens of *Progalago*, and the identity of the specimen is, therefore, somewhat uncertain. The single tooth is, however, approximately the same size as $M\overline{3}$ in specimen *R*.618, 1950, and thus the fragment has been provisionally included in *P. robustus*.

The mandible exhibits certain interesting divergencies from the conditions seen in modern galagos. Thus the coronoid process in the latter is strongly recurved with the tip of the process directed posteriorly (Pl. 3, figs. 12, 13). In the fossil specimen the coronoid process does not slope backwards, and the tip is directed upwards; it is also thicker and shorter than in the modern forms. Two ridges of bone, one passing downwards from the region of the coronoid process and the other passing forwards from the region of the angle of the mandible, converge to meet on the lateral side of the base of the ascending ramus, just posterior to the level of $M\overline{3}$. In the modern galagos, the site of convergence of these two bony ridges is marked by a distinct eminence, which may even be a definite tubercle. In the fossil, the muscular markings are not so pronounced and do not form an eminence at their point of juncture.

The angle of the mandible is not complete, but it can be seen to project well posterior to the level of the coronoid process. In the modern galagos the inferior border of the ramus curves markedly downwards as it approaches the angle; in the fossil specimens there is no such comparable downward curve. The lower border of the horizontal ramus is undamaged along the length of the fragment. It seems reasonable to infer that the features in which this mandible differs from that of the modern forms reflect differences, possibly of a yet more pronounced character, in the morphology of the skull.

Progalago minor sp. nov.

(Pl. 3, figs. 17, 18)

Diagnosis.—A species of *Progalago* in which the teeth are markedly smaller than in *P. dorae* and *P. robustus*. Length of the molar series approximately 7 mm. The molars show a close resemblance to those of *Galago demidovii* in size and cusp pattern, but they possess a better developed trigonid and antero-external angle. A weak external cingulum is developed on the anterior part of the lower molars. The species resembles *P. robustus* in the even depth of the mandible from front to back.

Holotype.—Posterior part of a right horizontal ramus of a mandible, containing all the molar teeth. Brit. Mus. (Nat. Hist.) M.16877. (Field No. *S*.103, 1949.)

Horizon.—Lower Miocene.

Locality.—Songhor, Kenya Colony.

Description and Remarks.—This species is represented by two mandibular fragments only, which resemble each other very closely, and consist of the posterior part of the horizontal ramus and the commencement of the ascending ramus. The holotype (Pl. 3, figs. 17, 18) is from the right side and possesses the three molars intact and unworn. Specimen *R*.611, 1949 (Site R1a), from the left side of a mandible, contains $M\overline{2}$ and $M\overline{3}$ and the posterior half of $M\overline{1}$. These molar teeth are markedly smaller than those of *P. dorae* and closely resemble in size the molars of the small *G.* (*Hemigalago*) *demidovii*.

The conformation of the molar cusps follows the same general plan seen in other species of *Progalago*. Thus the teeth are quadricuspid, with the protoconid and metaconid closer together than the entoconid and hypoconid. There is a well-developed trigonid, with a depressed talonid. The antero-external angle of the trigonid is prominent, but no paraconid is present. A crest joining the protoconid to the metaconid separates the smaller anterior moiety from the larger and lower posterior moiety of the crown. A moderately developed external cingulum is present on the anterior half of the teeth, especially on $M\overline{2}$. $M\overline{3}$ resembles the modern *G. demidovii* in possessing a distinct and well-marked entoconid, and in having the hypoconulid situated on the medial side of the median axis of the tooth. In neither specimen does the horizontal ramus increase in depth from before backwards, at least as far back as the posterior border of $M\overline{3}$.

The molars in these fossil specimens show a remarkable resemblance to the corresponding teeth in the modern *G. demidovii*; indeed, there appear to be only two main points of difference; the protoconid and metaconid are more closely approximated than are the entoconid and hypoconid, and secondly, in the fossils the trigonid region is better developed, with a more prominent antero-external angle. Apart from these two features, however, the similarity between the fossil and Recent species is striking.

GENERAL CONSIDERATION OF THE DENTITION OF *PROGALAGO*

The fossil material which has been described not only contributes substantially to our knowledge of the dentition of the Miocene precursors of the modern galago in East Africa, but makes it clear that these precursors were already at that time diversified into more than one species. Nine of the specimens have been assigned to the species *P. dorae* MacInnes (1943). In four other specimens the mandible does not show the significant increase in posterior depth which is characteristic of *P. dorae*. On the basis of this difference, together with certain details of the cusp pattern of the lower molars and the relative robustness of the mandible, these specimens have been assigned to a separate species *P. robustus*. The maximum thickness of the horizontal ramus of the holotype of *P. dorae* is 2·9 mm., as compared with a width of 2·8 mm. in the much smaller mandible (*S*.102, 1948) of *P. robustus*. Finally, two mandibular specimens clearly belong to a much smaller species, to which the name of *P. minor* has been given. In their size, proportions, and morphological details the molar teeth of *P. minor* closely resemble those of *G.* (*Hemigalago*) *demidovii*. They are more primitive in the conformation of the trigonid, which has a pronounced antero-external angle but no definite paraconid, and the protoconid and metaconid are closer together than are the entoconid and hypoconid. In general, however, it appears that the cusp pattern of the lower molars of *G. demidovii* has undergone very little change by comparison with the early Miocene species *P. minor*.

The upper dentition of *Progalago* is represented by two maxillary fragments, both of which can be assigned with reasonable certainty to *P. dorae*. The remnant of the lateral incisor in one specimen indicates a styliform tooth characteristic of many of the Recent lorisiforms, and the upper canine was of moderate size. The second and third upper premolars are quite similar to those of *Galago*. The upper molars show a simple tritubercular pattern, with only a small cingulum-hypocone on $M\underline{2}$ and none on $M\underline{3}$. In these features, as well as in the very slight reduction in size of $M\underline{3}$ by comparison with $M\underline{2}$, the upper molars of *P. dorae* are more primitive than those of *Galago*, approximating in this respect to the more generalized molar pattern still retained by some of the Recent Lorisinae.

It is unfortunate that no lower incisors or canines of *Progalago* have been found. However, in two mandibular specimens (*P. dorae R*.167, 1951 and *P. robustus* M.16876), sufficient of the symphysial region has been preserved, with remnants of the sockets, to show that these teeth were by no means so procumbent as those of the modern lorisiforms. It also seems certain that the canine had not become so completely assimilated to the incisor series.

In their total morphological pattern, the lower premolars resemble those of *Galago* more closely than those of any other Recent lorisiform; indeed, so far as dental criteria are concerned, they provide the main evidence for assigning these fossil lemurs to the sub-family Galaginae. The resemblances are: the forward angulation of the anterior margin of the protoconid and the spatulate form of $P\overline{2}$ and $P\overline{3}$, and the incipient molarization of $P\overline{4}$. When compared with those of *Galago* the premolars show certain primitive traits such as the smaller and less specialized $P\overline{2}$ and the lesser degree of molarization of $P\overline{4}$.

The cusp pattern of the lower molars of *Progalago* is generalized, and these teeth do not of themselves help much in deciding the taxonomic position of the fossil material, because the molars of Recent Lorisiformes are not very distinctive. In *P. dorae* and *P. robustus* they are somewhat more primitive than those of modern galagos of comparable size in the degree of approximation of the protoconid and metaconid, the relative size of $M\overline{3}$, and the larger size of the entoconid and the well-developed hypoconulid of $M\overline{3}$. On the other hand, the molar teeth of *P. minor* are very similar to those of the small species of *Galago*. They also resemble the lower molars of *Loris*. In *Progalago*, generally, the lower molars can be distinguished from those of *Nycticebus* by the presence in the latter of an external cingulum passing across the lower end of the groove between the protoconid and hypoconid. Among the other modern African lorisiforms, the lower molars of *Arctocebus* are characterized by the relatively large size of the anterior pair of cusps and by the presence of an oblique crest extending forwards and medially from the hypoconulid, and those of *Perodicticus* by the marked reduction of $M\overline{3}$, and the more quadrate form of $M\overline{1}$ and $M\overline{2}$.

In certain characters the teeth of *Progalago*, as already noted, resemble the Lorisinae rather than the Galaginae. Thus, the development of the entoconid and the hypoconulid on $M\overline{3}$, the relatively simple character of $P\overline{4}$, the absence of a deep notch in the posterior margin of the upper molars, and the well-marked diastema behind the upper canine, are approximations to *Nycticebus*. But these isolated resemblances are to be regarded as primitive lorisiform characters which have been lost in the modern galagos and not necessarily indicating a taxonomic relationship with those Lorisinae in which similar primitive features have been retained.

The only fossil lorisiform with which *Progalago* can be compared is *Indraloris* (Lewis, 1933). This genus is based on an isolated second molar tooth from the Lower Middle Siwalik horizon of India. This horizon is often regarded as Lower Pliocene (Colbert, 1935), and thus considerably later than the East African deposits. When he placed *Indraloris* among the Lorisinae, Lewis was impressed by the numerous resemblances between his specimen and the second molar of *Nycticebus*, particularly the disposition of the cusps, the presence of a well-marked anterior fovea, and the strong development of the external cingulum between the protoconid and hypoconid, and he suggested that *Indraloris* probably represents the "structural ancestor" of Recent Lorisinae. In its much smaller size, in the absence or only moderate development of the external cingulum, and in the less strongly marked anterior fovea, the second molar of *Progalago* differs from that of *Indraloris*, and shows a closer resemblance to *Galago*. The breadth index of the *Indraloris* tooth (78·1) is also much lower than that of *P. dorae*. If Lewis is correct in concluding that *Indraloris* represents a precursor of the Lorisinae, it is evident that the Lorisinae and Galaginae had diverged by the Lower Pliocene, and the morphological resemblances between *Progalago* and *Galago* suggest further that this divergence had already occurred by early Miocene.

In his original description, MacInnes (1943) compared *P. dorae* with the Eocene tarsioids *Necrolemur* and *Microchoerus*. The additional material now makes it clear that the resemblances are outweighed by the numerous differences. In *Necrolemur* a paraconid is present on $M\overline{1}$, the lower incisors have disappeared, the full complement of lower premolars is retained, and the upper molars have a well-developed hypocone. In *Microchoerus* the quadritubercular upper molars are complicated by a number of secondary cuspules. Two Eocene tarsioids, *Pronycticebus* and *Pseudoloris*, have generic names which suggest a relationship to the Lorisiformes, but the first of these is a true lemuriform (Le Gros Clark, 1934), and the dentition of *Pseudoloris* bears such a close resemblance to *Tarsius* that Teilhard de Chardin (1921) suggested *Protarsius* as a more appropriate generic name.

The differences in size between the teeth of the species of *Progalago* parallel those between the Recent species of *Galago*, and indicate that by early Miocene times the Galaginae had already become as widely diversified in general body size.

Progalago sp.

(Pl. **1**, figs. 1, 2; Pl. **2**, fig. 3)

Skull

Mention has already been made of two maxillary fragments of *P. dorae*, one of which suggests a skull of rather lighter construction than that of Recent species of *Galago* with teeth of comparable size. In a mandible of *P. robustus*, also, the ascending ramus and coronoid process reveal differences which are taken to reflect corresponding differences in the skull as a whole. In 1950, Dr. Leakey found on Rusinga Island (site R3) a portion of a skull, with an endocranial cast, which can be assigned with confidence to one of the larger species of *Progalago*. The jaws and teeth are missing; hence it is not possible to say whether the skull should be referred to *P. dorae* or to *P. robustus*.

The specimen (*R*.1005, 1950) comprises an almost complete natural endocranial cast, but of the skull itself only the posterior half of the calvaria and part of the base are preserved. Approximately the posterior two-thirds of the parietal bones are present, as well as the greater part of the occipital bone. The base of the skull includes the tympanic region, the basi-occipital and basi-sphenoid elements, and portions of the occipital condyles. The main dimensions of the skull are: maximum antero-posterior length (measured from the anterior pole of the endocranial cast), 27·3 mm.; maximum width, 24·7 mm.; maximum height (measured from the anterior margin of the basi-occipital bone), 13·0 mm.

On the dorsal aspect of the skull (Pl. 1, fig. 1) the sagittal and lambdoid sutures can be clearly distinguished. Compared with modern galago skulls of the same size, the lambda is situated relatively farther forwards on the vertex of the skull, approaching in this respect the condition seen in *Perodicticus* and *Nycticebus*. The distance between it and the tip of the occipital protuberance is approximately 7 mm. The temporal ridges are well marked and widely separated throughout their course. In this feature they differ from the larger species of *Galago*, in which the ridges approximate closely in the posterior parietal region, but resemble the smaller species of *Galago* and the Lorisinae. As they pass backwards, the ridges converge slightly as far as the lambdoid suture where they are separated by an interval of 13 mm. They then turn laterally along the line of the suture and finally pass forwards and downwards, immediately above the auditory aperture, to the root of the zygomatic process. The nuchal area of the occipital bone is flattened, and shows a prominent and strongly marked nuchal crest which extends transversely across the back of the skull, turning down towards the mastoid region on either side.

The lateral aspect shows the marked flattening of the dome of the skull (Pl. 1, fig. 2). This is one of the most distinctive features of the fossil and contrasts with the evenly arched convexity of the dome in the skulls of modern galagos. The flattening does not appear to be the result of post-mortem deformation. The auditory aperture is clearly outlined, with a maximum antero-posterior diameter (measured on the left side) of 3·2 mm., and the auditory bulla forms a prominent rounded projection on the base of the skull. The squamo-parietal suture is about 4 mm. above the upper margin of the auditory aperture.

The most interesting features are on the basal aspect of the skull (Pl. 2, fig. 3). The auditory bullae are almost intact, though the right side is slightly distorted. In their prominent, rounded and circumscribed form, they closely resemble the modern galagos (particularly the medium-sized species such as *G. senegalensis*). On the other hand, they contrast rather strongly with all other lorisiforms, in which the bulla is relatively much smaller and less inflated. Compared with *Galago*, the bulla of *Progalago* appears to be more strongly circumscribed posteriorly, because in the former its surface contour tends to merge with the markedly inflated mastoid region. The postero-medial surface slopes steeply, whereas the postero-lateral surface slopes more evenly and gradually upwards to the auditory aperture. There is no trace of a tubular meatus, even in the incipient form which is found in *Nycticebus*, *Arctocebus* and, to a very slight extent, in *Loris*. The composition of the auditory bulla is of some importance for the determination of the systematic affinities of the lower primates; this is particularly true of the extent to which the ectotympanic element enters into the formation of the bulla. Immediately within the auditory aperture of the fossil, on the left side, a small extent of the groove (sulcus tympanicus) for the attachment of the tympanic membrane is present. Clearly, therefore, the tympanic annulus was not enclosed as a free element within the bulla. On the contrary, as is characteristic of the Lorisiformes generally, the ectotympanic element evidently contributed to the formation of the lateral wall of the bulla. About 2 mm. above and lateral to the tympanic sulcus is an indistinct groove, which can be traced backwards behind the auditory aperture on to the surface of the bulla. This groove is taken to mark the junction between the upper and posterior part of the ectotympanic and the squamous portion of the temporal bone. On the convexity of the bulla there is no very evident change in texture of the bone near the auditory aperture to indicate the limit of the ectotympanic element. However, this limit is often difficult to detect in the adult skull of modern lorisiforms, and in this specimen of *Progalago* it has evidently been still further obscured in the process of fossilization. Nevertheless, it is reasonably certain that *Progalago* resembles the modern lorisiforms in that the ectotympanic element helps to form the lateral wall of the bulla.

Close up against the posterior margin of the auditory aperture, at the extreme postero-lateral point of the bulla, is a conspicuous stylo-mastoid foramen on the left side, but the foramen on the right side is not so distinct. Behind the bullae the foramen lacerum posterius can be identified on either side, although on the right side the medial part of the foramen is absent. There is no sign of a hypoglossal canal. A minute foramen is present at the extreme posterior end of the bulla, slightly to the medial side. It can be clearly observed on the right, but on the left it has been somewhat compressed by distortion of the bulla. This foramen, situated directly lateral to the foramen lacerum posterius, almost certainly represents the site of entry into the bulla of the stapedial branch of the entocarotid artery. There is no evidence of a posterior carotid foramen, such as is seen in the Lemuriformes. It is thus not unreasonable to suppose that there must have been a foramen lacerum medium through which the vessel corresponding to the arteria promontorii division of the entocarotid artery entered the skull. Such an arrangement is characteristic of the Lorisiformes.

On the left side of the fossil post-mortem damage has exposed some of the mastoid air cells. One of the most striking differences between the modern galagos and the fossil is the very limited extent to which in the latter the mastoid region is inflated with air cells: in *Galago*, *Perodicticus* and *Arctocebus* an extensive inflation forms a marked prominence lateral to the occipital condyle. In *Nycticebus* and *Loris* the mastoid region is but little inflated and in this respect these lorisiforms more closely resemble *Progalago*.

The sutures between the auditory bulla and the basi-occipital and basi-sphenoid, and also the articulation between the basi-occipital and the basi-sphenoid (Pl. 2, fig. 3), are clearly defined. Since the sphenoid bone is missing, apart from the basi-sphenoid element, the presence of a foramen lacerum medium cannot be directly determined, but the antero-medial portion of the bulla extends forwards as a blunt, tongue-like projection in a manner very similar to that seen in the modern galagos.

A small rectangular portion of the basi-occipital bone is preserved at its articulation with the basi-sphenoid, and the line of contact occupies relatively the same position as it does in *Galago*.

Only the posterior portions of the occipital condyles remain, and they have been much damaged. In the modern galagos the longitudinal axes of the condyles are somewhat obliquely disposed, diverging posteriorly. There is some indication that the condyles were disposed differently in relation to the foramen magnum in the fossil, for their posterior extremities, instead of being directed laterally as in the modern forms, appear to be directed medially, and to be more posteriorly extended around the margin of the foramen magnum.

On the left side of the base of the skull a small medial portion of the mandibular fossa has been preserved, but this is unfortunately not sufficient to indicate the conformation of the mandibular joint. The region of the post-glenoid process and foramen is missing.

In spite of its fragmentary nature, this specimen is of considerable importance because it is the first fossil lorisiform skull so far discovered. Its lorisiform character is determined by the relation of the ectotympanic element to the auditory bulla and by the disposition of the foramina on the base of the skull. In the prominent and circumscribed appearance of the bulla, it shows a closer resemblance to *Galago* than to any other Recent lorisiforms, and there can be no reasonable doubt that the specimen is the skull of *Progalago*. On the basis of its size it is referable either to *P. dorae* or to *P. robustus*.

The skull is more primitive than that of modern galagos of comparable size in a number of characters, including the wider separation of the temporal ridges, the flattening of the roof of the skull and of the occipital region, and the absence of a pronounced inflation of the mastoid region. In its general character the skull thus agrees with the dentition in displaying galagine resemblances combined with features which are certainly more primitive than those of modern galagos. On the other hand, it is much more advanced in its development than that of any of the Eocene lemuroids, particularly in the expansion of the neurocranium. It should be emphasized that all the known Eocene lemuroid skulls are referable to the Lemuriformes.

Endocranial Cast (Text-fig. 2)

After the study of the skull (*R*.1005, 1950) had been completed, the right side of the cranial wall was removed from the surface of the endocranial cast as far as possible. The cast proved to be perfectly preserved except on the basal aspect, but the olfactory bulbs are not represented. Lateral and dorsal views of the cast are shown in text-fig. 2, compared with the endocranial cast of *G. senegalensis*, which has a skull of comparable size. The maximum length of the fossil cast from the frontal poles of the cerebral hemisphere is 26·8 mm., and its maximum width 23·6 mm. Its vertical height at the level of the anterior margin of the remaining part of the basi-sphenoid bone is 10·2 mm.

Seen from the lateral aspect, the cerebral hemispheres appear markedly flattened in comparison with the endocranial cast of the modern galago. The temporal lobe also is not so prominently developed, though the tip of the temporal pole may have extended down for a further 1–2 mm. in the undamaged specimen. The vallecula Sylvii forms a well-defined groove between the temporal pole and the orbital region of the frontal lobe, but it does not extend on to the dorsal surface of the hemisphere as a definite sulcus. The occipital pole is not so prolonged backwards over the cerebellum as it is in *Galago*.

Seen from above, the hemispheres are smooth, except for a shallow antero-posterior depression over the surface of the frontal region, which evidently marks the position of a short sulcus. The frontal lobes are obtusely rounded anteriorly and contrast with the rather pointed frontal poles of *Galago*. When viewed from the dorsal aspect, this gives an impression that the frontal lobes were actually better developed than in Recent forms. Such an impression is deceptive, for in the fossil the lobes are much attenuated by a dorsi-ventral flattening. The vermis of the cerebellum is prominent, and marked by transverse sulci. It is separated on either side from the lateral lobes of the cerebellum by a relatively deep sulcus.

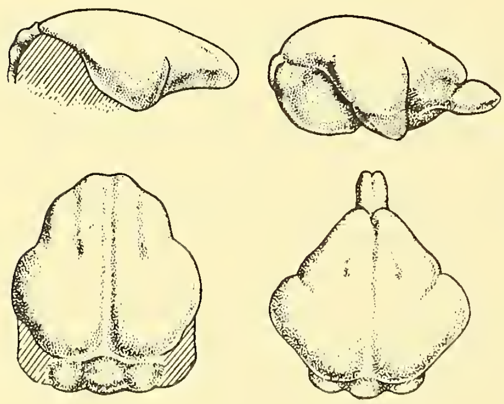

FIG. 2. The endocranial cast of (A) *Progalago sp.* compared with that of (B) *G. senegalensis*, viewed from the lateral and dorsal aspects. Approximately natural size.

In general, the brain of *Progalago* was more primitive than that of the modern galagos in the flattening of the cerebral hemispheres, in the less pronounced development of the temporal lobes, and in the degree to which the cerebellum remains exposed behind the occipital poles. On the other hand, it is more advanced than that of the Eocene lemuroid *Adapis parisiensis*, for in the latter the cerebellum appears to have been almost entirely uncovered by the occipital lobes of the cerebral hemisphere, and the frontal lobes were relatively much smaller (Le Gros Clark, 1945). The antero-posterior sulcus on the dorsal surface of the cerebral hemisphere is actually longer and more conspicuous on the endocranial cast of *Adapis* than on that of *Progalago*, but this may be related to the larger size of the Eocene animal. The size of the olfactory bulbs in *Progalago* cannot be directly assessed; but so far as can be judged by the contour of the preserved extremities of the frontal poles, they were almost certainly smaller than in *Adapis*.

Knowledge of the brain in different groups of fossil mammals is still very meagre, in spite of the extensive studies made by Edinger (1929, 1948). However, the evolution of the brain in the Equidae may be used in comparison. The brain of *Merychippus* (middle and upper Miocene) was still very small compared with that of *Equus*, even though *Merychippus* was as big as a modern Shetland pony. In other words, the contrast between the brain development of Miocene and modern representatives of the Equidae is much more marked than that between *Progalago* and *Galago*. This comparison, together with collateral evidence provided by the skulls of Eocene tarsioids, suggests that the expansion of the brain proceeded more rapidly in the earlier stages of primate evolution that it did in some other groups of mammals. The endocranial cast of *Progalago*, even without the evidence of the skull, is definitely recognizable as that of a small primate and, in spite of its primitive characters, approaches very closely in form and proportions that of the modern *Galago*.

DISCUSSION

It is clear from the fragmentary remains described in this paper that during the early Miocene period East Africa was already inhabited by small lemuroids akin to the modern galago, and that there were several species showing a marked contrast in general size. Their precise relationship to Recent Galaginae must remain obscure until more complete evidence, particularly concerning the post-cranial skeleton, is available. MacInnes suggested that these East African lemuroids may represent the ancestral stock from which *Galago* was derived, hence the generic name *Progalago*. The material so far available provides no morphological argument against this interpretation; indeed, *Progalago* presents a number of morphological features which conform reasonably well with theoretical postulates for an early Miocene member of the Galaginae, in that they are primitive characters which were presumably antecedent to the more specialized characters of the modern galagos. As already noted, these features include the incipient molarization of $\overline{P4}$, the moderate procumbency of the incisors; the incomplete assimilation into the incisor series of the lower canine, either in its relative size or its position; the small size of the hypocone in the upper molars, with the absence of the characteristic indentation of the posterior margin of these teeth; the more generalized cusp pattern of the lower molars, with no reduction in the size of $\overline{M3}$; the slight degree of inflation of the mastoid region of the skull and the less advanced development of the brain. Notwithstanding these primitive features, however, the Miocene genus *Progalago* approximates closely in the total morphological pattern presented by the dentition, skull and endocranial cast to the modern genus *Galago*. The infra-order Lorisiformes had evidently become differentiated by the early Miocene, and the sub-family Galaginae was already established as a separate evolutionary sequence.

Between the Miocene *Progalago* and the known Eocene lemuroids there is a conspicuous gap in the palaeontological record of the Lemuroidea. From their skull-characters the Eocene genera *Adapis*, *Pronycticebus* and *Notharctus* are all early representatives of the Lemuriformes, for they show the characteristic structure of the auditory bulla and the same disposition of foramina in the base of the skull. In these characters the Lorisiformes contrast rather strongly with the Lemuriformes, and this is commonly assumed to indicate a morphological and evolutionary divergence at least as far back as Eocene times. If this inference is correct, however, it necessarily follows that since their evolutionary divergence both groups must have developed independently a remarkable number of parallel characters, such as the specialization of the lower incisors and canines to form a "dental comb", which had not yet appeared in the Eocene lemuriforms. The possibility remains, however, that the contrasting features in cranial morphology in the two infra-orders of the Lemuroidea may not be so fundamentally divergent as some taxonomists have supposed. Indeed, according to Gregory (1920), the lemuriform type of auditory bulla, constructed from an entotympanic element enclosing a free ectotympanic ring, represents a primitive stage of evolutionary development which gave rise to the more specialized types of bulla characteristic of other groups of primates. Moreover, in a recent study of the skull of *Necrolemur*, Hürzeler (1948) appears to have demonstrated that, contrary to previous suppositions, the morphology of the auditory bulla and the ectotympanic element conform to the "lemuriform" type rather than to that characteristic of the Recent *Tarsius*. Yet *Necrolemur* presents many other morphological characters of the skull and dentition which justify its recognition as an early tarsioid. This important observation raises the question whether the morphology of the auditory region in *Necrolemur* may not have been antecedent to the condition which later was developed in *Tarsius*. It thus has a direct relevance to the origin of the Lorisiformes, for it suggests the possibility that the latter may have been derived from one of the groups of Eocene lemurs, even though the tympanic region of the skull displays characters which are regarded as distinctive of the Lemuriformes. The answer to this problem can only be provided by further accessions of palaeontological material.

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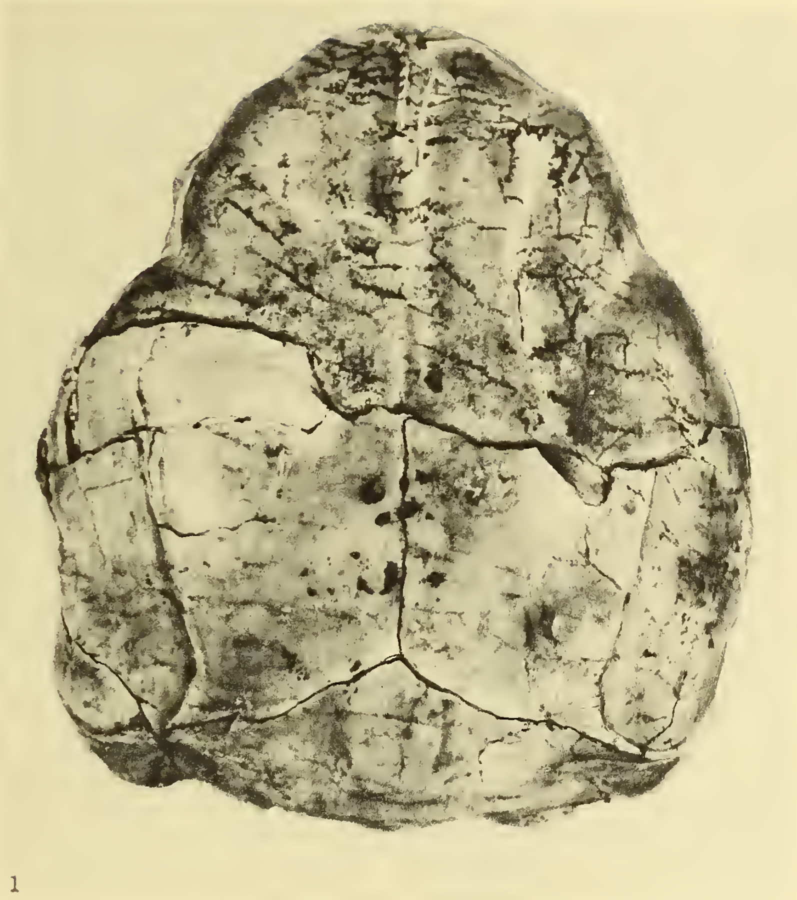
EXPLANATION OF PLATES

PLATE 1

EXPLANATION OF PLATE 1

FIG. 1. Skull and endocranial cast of *Progalago* sp. (*R*.1005, 1950), viewed from above. ×4.

FIG. 2. The same specimen viewed from the left side. ×4.



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PROGALAGO

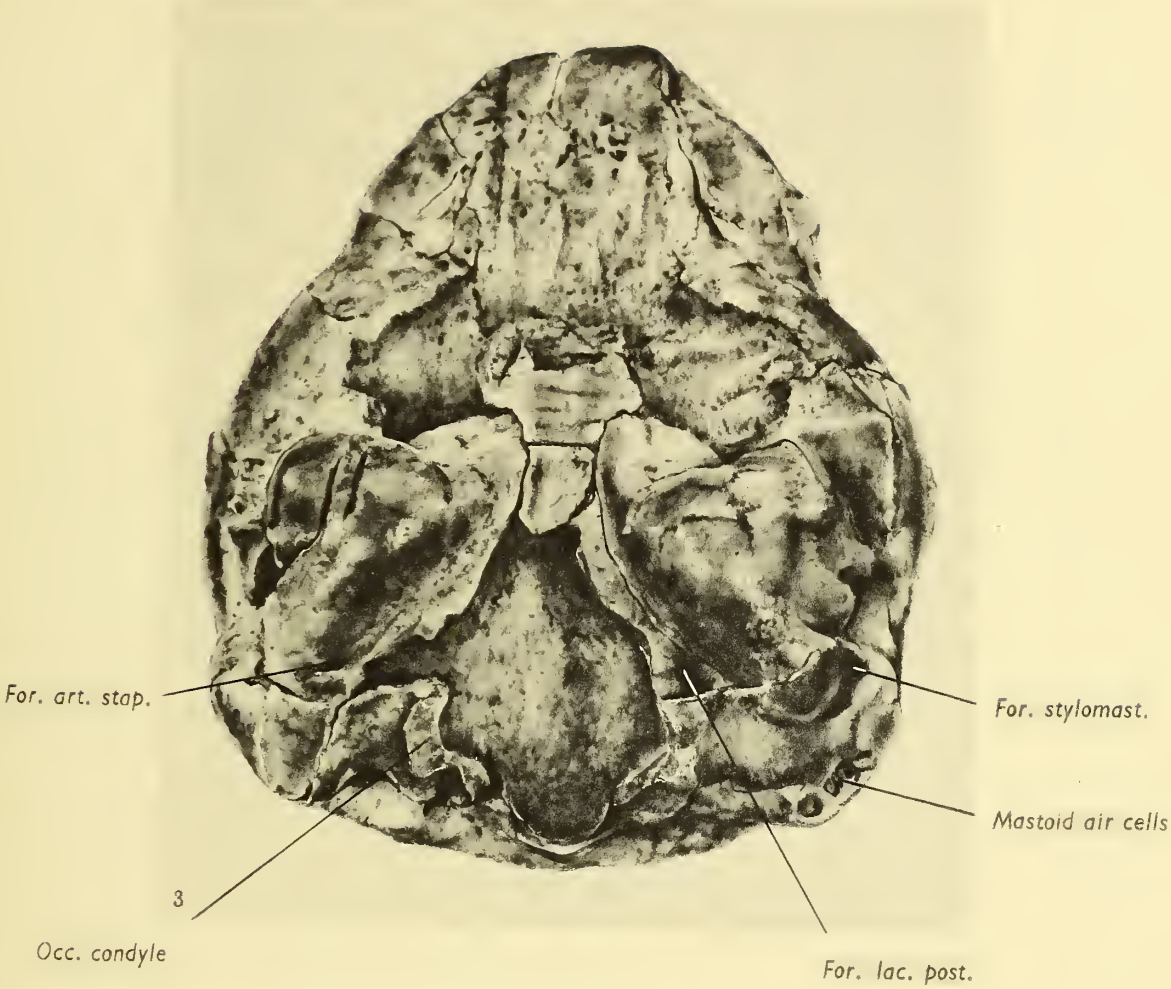
PLATE 2

EXPLANATION OF PLATE 2

FIG. 3. Basal aspect of skull of *Progalago* sp. (*R*.1005, 1950). ×4.

FIG. 4. Fragment of left side of mandible of *P. dorae* with $P\bar{2}$ and $M\bar{2}$ (holotype), viewed from the medial aspect. ×4·5.

FIG. 5. The same specimen viewed from above. ×4·5.



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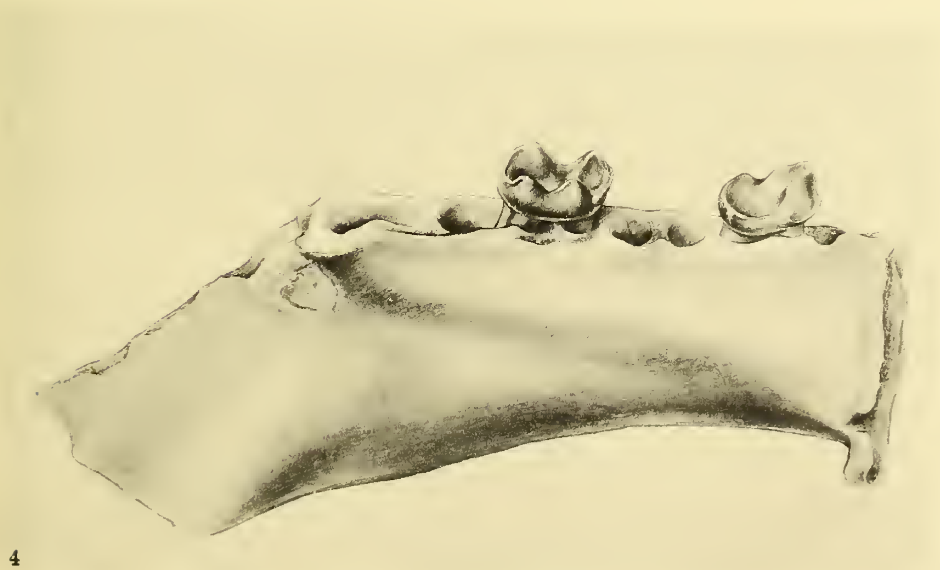

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PROGALAGO

PLATE 3

EXPLANATION OF PLATE 3

FIG. 6. Fragment of right side of mandible of *Progalago dorae* with the three premolars (*S*.310, 1949), viewed from the medial aspect. ×4.

FIG. 7. Fragment of left side of mandible of *P. dorae* (*S*.10, 1949) with $M\bar{2}$ and $M\bar{3}$, viewed from the lateral aspect. ×4.

FIG. 8. The same specimen showing the occlusal aspect of $M\bar{2}$ and $M\bar{3}$. ×4.

FIG. 9. Fragment of right maxilla of *P. dorae* with $I\underline{2}$, C, $P\underline{2}$ and $P\underline{3}$ (*S*.93, 1948), viewed from the lateral aspect. The incisor and canine have been severely damaged and only the stumps remain. ×3.

FIG. 10. Fragment of left maxilla of *P. dorae* (*R*.106, 1948), showing the occlusal aspect of $M\underline{2}$ and $M\underline{3}$. ×3.

FIG. 11. (a) Left $M\bar{3}$ of *P. dorae* (*S*.10, 1949) compared with (b) that of *G. crassicaudatus*. Both teeth are shown from the lingual aspect. Note the stronger development of the entoconid and hypoconulid in the fossil specimen. ×3·5.

FIG. 12. Fragment of right side of mandible of *P. robustus* (*S*.8, 1948), viewed from the lateral aspect, with $M\bar{3}$ in position. ×4.

FIG. 13. Posterior part of right side of mandible of *G. senegalensis* for comparison with the previous specimen. ×4. Note the difference in the shape of the coronoid process and in the muscular ridges.

FIG. 14. Fragment of right side of mandible of *P. robustus* with $P\bar{3}$, $P\bar{4}$, $M\bar{1}$ and $M\bar{2}$ (M.16876), viewed somewhat obliquely from above. In front are seen the sockets for the two incisors, the canine and $P\bar{2}$. ×4.

FIG. 15. Fragment of right side of mandible of *P. robustus* (*R*.618, 1950), viewed from the lateral aspect with the three molars in position. ×4.

FIG. 16. Occlusal aspect of left $M\bar{1}$ and $M\bar{2}$ of *P. robustus* (M.16876). ×4.

FIG. 17. Fragment of right side of mandible of *P. minor* (M.16877) with the three molars in position. ×4.

FIG. 18. The same specimen viewed from the occlusal aspect of the teeth. ×4.

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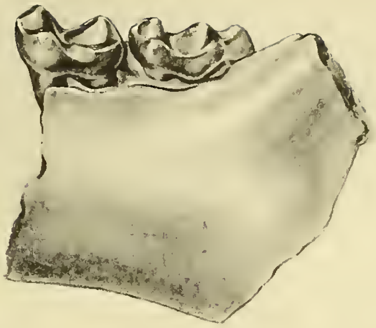

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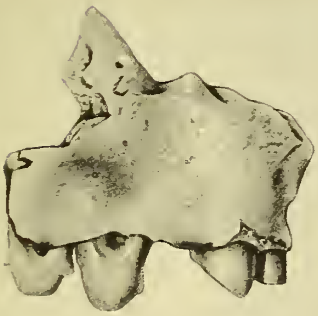

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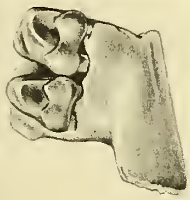

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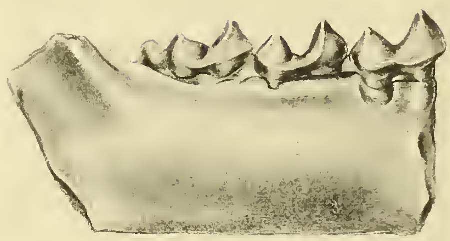

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PROGALAGO